THE EUSPORANGIATE FERNS AND THE STELAR THEORY

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Some thirty years ago, as the result of an extensive series of investigations, Van Tieghem, the distinguished French botanist, brought forward his stelar theory which offered an interpretation of the nature of the tissue systems of the higher plants quite different from that which had been held by Sachs, de Bary, and other earlier investigators.

Van Tieghem's views, with some more or less important modifications, have been pretty generally accepted by the morphologists of the past two decades, and have been assumed to apply to all the vascular plants.

Among the forms which have been the subjects of frequent and detailed study in regard to the nature of their stelar structures are various ferns. These studies have been directed largely toward the elucidation of the evolution of the stelar structures of the Filicineae and have included a study of many fossil ferns as well as the existing types. These investigations have thrown much light upon the relationships existing between the many Palaeozoic fern-like plants and their living relatives.

An extensive literature on the subject has grown up in the past twenty years, especially in England, and with it a somewhat elaborate terminology based upon the assumption that the fibro-vascular skeleton of the fern stem is a strictly cauline "stele" with which the corresponding foliar bundles are simply connected by the so-called "leaf-traces."

The general acceptance of Van Tieghem's stelar hypothesis and its modification by Strasburger and other investigators, especially in England, are sufficiently familiar to students of plant anatomy. Van Tieghem concerned himself chiefly with the Spermatophytes, and his interpretation of the stelar structures of the ferns has been a good deal modified by the English investigators and by Jeffrey in this country. The latter[1] has summarized these conclusions, and this has also been done at length by Bower[2] and Schoute.[3]

Some of the most recent contributions to the subject[4] apparently accept these views as applying universally to the ferns, and quite ignore the evidence brought forward by the writer nearly ten years ago,[5] and amply

[1] Jeffrey, E. C. The structure and development of the stem in Pteridophyta and Gymnosperms. Philos. Trans. Roy. Soc. B, **195**: 119–146. 1902.

[2] Bower, F. O. The origin of a land flora. London, 1908.

[3] Schoute, J. C. Die Stelär-Theorie. Jena, 1903.

[4] *E.g.*, Thompson, J. M. New stelar facts, and their bearing on stelar theories for the ferns. Trans. Roy. Soc. Edinburgh **52**: part 14, no. 28. 1920.

[5] The Eusporangiatae. Carnegie Inst. Washington Pub. 140. 1911.

verified by the more recent work of West,[6] that the stelar theory, as usually understood, cannot be reconciled with the facts as revealed by a study of the Eusporangiatae. The writer has therefore thought it worth while to summarize this evidence, and also to add further facts derived from a recent study of Botrychium.

From an extensive series of investigations on nearly all the genera of eusporangiate ferns, the writer was forced to the conclusion that a cauline stele is either completely wanting in these ferns, or that, where cauline stelar tissues are present, they constitute an insignificant part of the fibro-vascular skeleton. West's studies on the Marattiaceae confirm these conclusions, which, however, as already indicated, seem to have been quite overlooked by some of the recent investigators.

According to Van Tieghem's view, most of the ferns are "polystelic," the individual strands of the net-like woody cylinder of the stem being considered to be of independent origin, the reticulate structure resulting from the coalescence of these independent "steles." Most of the later students of the ferns consider the "dictyostele," or reticulate woody cylinder, to be a single structure, *i.e.*, the stem is regarded as "monostelic," the openings being designated "leaf-gaps" where the leaf-traces join the cylindrical cauline stele. In nearly all the recent studies on the stelar structures of the ferns, the strictly cauline nature of the axial fibro-vascular tissues is apparently taken for granted.

Brebner[7] first pointed out that in the very young sporophyte of *Danaea simplicifolia* the primary fibro-vascular bundle is common to the cotyledon and root, and that for a considerable time there is no evidence of any cauline stele. Little attention has been paid to these facts by most recent students of the ferns, but in a recent paper by West[8] the accuracy of Brebner's conclusions has been fully recognized.

The writer's attention was first called to the real state of affairs in the Eusporangiatae as the result of a study of the embryology of *Ophioglossum Moluccanum.*[9]

Many years ago, Mettenius[10] described the young sporophyte of *Ophioglossum pedunculosum* as consisting at first simply of a leaf and root, the definitive sporophyte arising secondarily as a bud upon the primary root. Very little attention was given by later students of the Ophioglossaceae to this really remarkable discovery, and it has been either forgotten or ignored.

The writer collected in Java a considerable number of young sporophytes

[6] West, C. A contribution to the study of the Marattiaceae. Annals of Bot. **31**: 361–414. 1917.

[7] Brebner, G. On the prothallus and embryo of *Danaea simplicifolia*, Rudge. Annals of Bot. **10**: 109–122. 1896. On the anatomy of Danaea and other Marattiaceae. Annals of Bot. **16**: 517–552. 1902.

[8] *Loc. cit.*

[9] Studies on the Ophioglossaceae. Ann. Jard. Bot. Buitenzorg II, **6**: 138–194. 1907.

[10] Mettenius, G. Filices Horti Botanici Lipsiensis. Leipzig, 1856.

of *O. Moluccanum* Schlecht, which is possibly identical with *O. pedunculosum* Desv. Specimens were secured in Ceylon of *O. reticulatum* L. or some closely related species. These agreed closely with the species described by Mettenius, and indicated that in these tropical species of Euophioglossum, the young sporophyte is absolutely destitute of any cauline tissues, being composed at first of a simple primary leaf, or cotyledon, which merges insensibly into the root (fig. 1). A single central fibro-vascular bundle or "stele" extends without interruption from the petiole into the root, and its structure is essentially the same throughout, *viz.*, "collateral" in the petiole, "monarch" in the root.

Mettenius does not describe in detail the origin of the different organs of the embryo sporophyte. In *O. Moluccanum* the writer found that the sporophyte at a very early stage consists of but two portions, a large basal

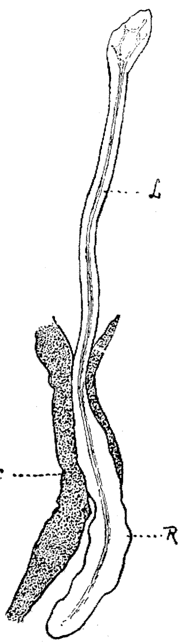

FIG. 1.

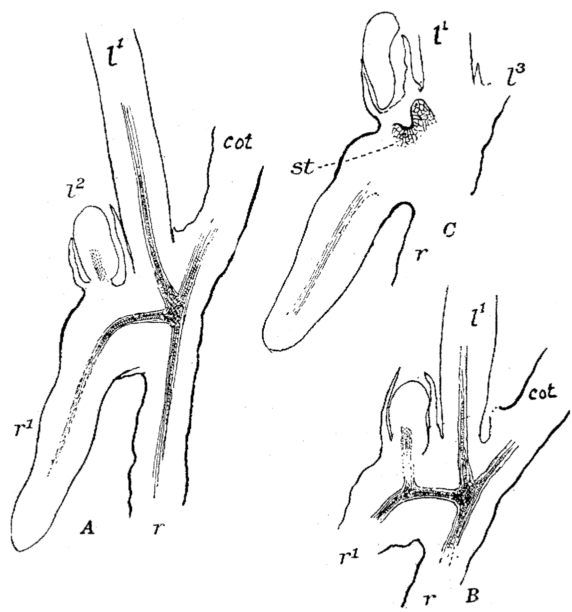

FIG. 2.

FIG. 1. Median longitudinal section of a young sporophyte of *Ophioglossum Moluccanum*, showing the primary stele traversing the cotyledon, *L*, and the root, *R*. *Pr*, the gametophyte.

FIG. 2. Three longitudinal sections of the bud developed upon the primary root, *r*, of *Ophioglosum Moluccanum*. *cot*, cotyledon; l^1, l^2, the first two leaves of the bud; r^1, the first root of the bud; *st*, the stem apex.

foot and an apical conical portion developing subsequently into the cotyledon. At this stage, the embryo is strongly suggestive of that of Anthoceros. The growing point of the primary root arises endogenously, being formed near the center of the embryo where the base of the young cotyledon

joins the foot. As the root grows, it pushes downward through the foot, which is practically eliminated and is no longer recognizable. The young sporophyte is thus bipolar in structure, and the stele, as we have seen, is continuous through the cotyledon and root.

It is not until the cotyledon and primary root are fully developed that the bud which is to develop into the definitive sporophyte first becomes evident. This begins as a group of meristematic cells close to the stele of the root—exactly in the way a secondary root arises. The first two leaves of this bud are formed quite independently of the apical meristem of the young bud. The stele of the first leaf of the bud joins directly with the stele of the primary root, while that of the second leaf is joined to the base of the stele of the first root developed from the bud (fig. 2).

It is thus clear that the fibro-vascular system in the sporophyte of *O. Moluccanum* begins as a single continuous strand extending from the petiole of the cotyledon into the primary root and practically of the same structure throughout, the xylem and phloem of the "collateral" foliar portion being continuous with the corresponding tissues of the "monarch" root portion. This primary "stele" is not a "protostele," *i.e.*, it is not "concentric" in structure, and, moreover, it is not a cauline structure.

A study of the older sporophyte shows that much the same condition prevails as in the earlier stages. The leaf-traces unite with root bundles and with the older leaf-traces, and there is thus built up the open "dictyostele" found in the adult rhizome.[11] There is no indication of the development of any stelar tissues except those belonging either to the leaves or to the roots.

Botrychium

In *Botrychium Virginianum* the structure of the axial stele is quite different from that in Ophioglossum. At an early stage,[12] the axis of the young sporophyte shows an almost unbroken cylindrical stele enclosing a central pith instead of the large-meshed "dictyostele" of Ophioglossum. In the very young sporophyte a single strand of procambium extends through the axis of the cotyledon into the primary root; but as these organs usually make a marked angle with each other, the primary vascular strand is strongly bent instead of being straight, as it is in *Ophioglossum Moluccanum*. Very soon the second leaf is developed, and a similar vascular strand is formed in it, which unites with the primary vascular bundle near the point of junction between the petiole of the cotyledon and the base of the primary root (fig. 3), and the fusion of the three bundles appears as a closed ring in cross section.

The traces from the later leaves behave in much the same way, and the massive "siphonostele" found in the older stem is thus built up.

[11] For details see "The Eusporangiatae," pp. 89–93.

[12] Jeffrey, E. C. The gametophyte of *Botrychium Virginianum*. Trans. Canad. Inst. **5**: 1–32, 1898.

As in Ophioglossum, the bundles are collateral, and, as is well known, there is developed a cambium between xylem and phloem, and also medullary rays, so that the structure of the woody cylinder in the older sporophyte is extraordinarily like that in the Gymnosperms and in many Dictoyledons.

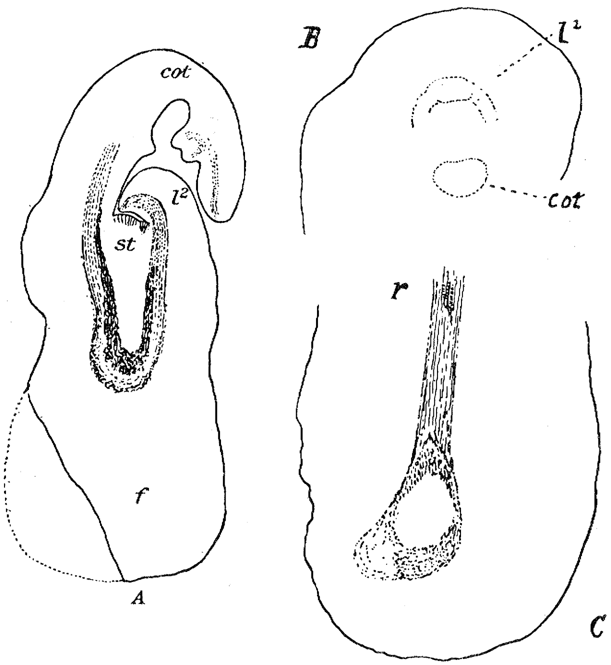

FIG. 3. *A*. Median longitudinal section of a young sporophyte of *Botrychium Virginianum*, cut at right angles to the primary root. The two leaf-traces unite at the junction of the root. *B*. Transverse section of a similar sporophyte showing the two leaf-traces. *C*. Another section of the same sporophyte showing the junction of the two leaf-traces with the stele of the root.

As in Ophioglossum, there is also in Botrychium no evidence of any procambial tissue in the axis above the youngest leaf-trace, *i.e.*, the stelar tissues as in Ophioglossum are composed entirely of the coalescent leaf-traces.

A still closer resemblance to Ophioglossum is shown by the young sporophyte of *B. obliquum* Mühl., which the writer has recently examined. In this species the cotyledon and primary root, instead of forming an angle with each other, as in *B. Virginianum*, have a common axis, and the orientation of these organs is like that in *Ophioglossum Moluccanum*. The writer is indebted to Dr. H. L. Lyon of Honolulu for the material upon which his investigations were made, and for the accompanying photograph (fig. 4).

Dr. Lyon[13] first directed attention to the peculiarities of this species,

[13] Lyon, H. L. A new genus of Ophioglossaceae. Bot. Gaz. **40**: 455–458. 1905.

and through his courtesy the writer has been able to examine a large number of preparations made by Dr. Lyon, as well as to make a series of slides from gametophytes and sporophytes furnished by him.

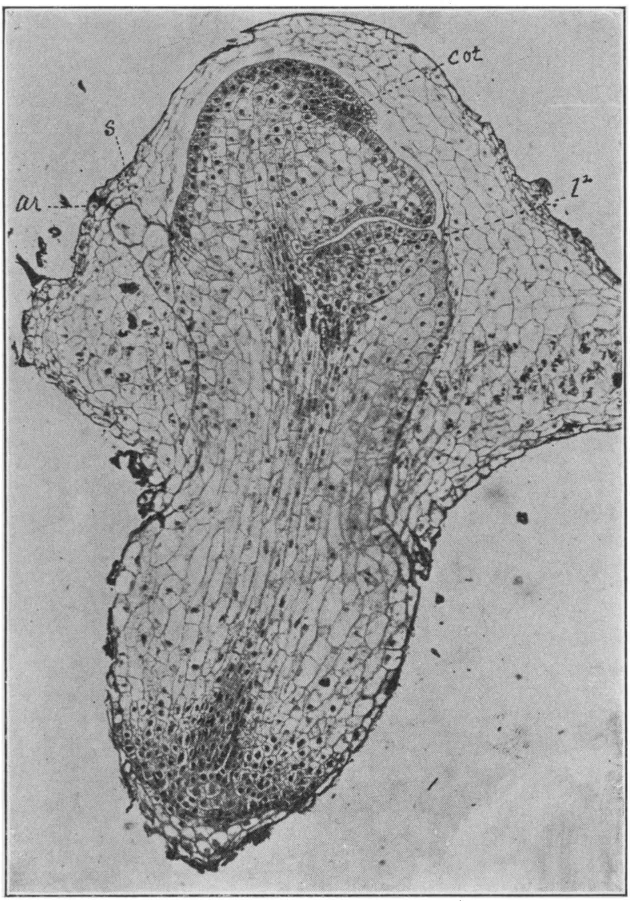

FIG. 4. Median longitudinal section of a young sporophyte of *Botrychium obliquum*, showing the continuity of the steles of the cotyledon and root, and the junction of the two leaf-traces at the base of the root. Photograph by Dr. H. L. Lyon.

In *B. obliquum* (fig. 4), there is a conspicuous suspensor, comparable to that in Danaea[14] and Macroglossum.[15] Moreover, the young sporophyte is bipolar in structure, and the relation of cotyledon and root is essentially the same as in *Ophioglossum Moluccanum*. As in the latter, the primary root of *Botrychium obliquum* is endogenous in origin, instead of being superficial as it is in *B. Virginianum*. It grows downward through the foot, exactly

[14] Campbell. The Eusporangiatae.

[15] Campbell, D. H. The structure and affinities of *Macroglossum Alidae*, Copeland. Annals of Bot. **28**: 651–669. 1914.

as it does in *Ophioglossum Moluccanum* and the Marattiales, and the foot thus is practically obliterated, instead of forming a large part of the embryo as it does in *B. Virginianum*. In the latter, as we have seen, the primary root and the cotyledon make a sharp angle with each other, while in *B. obliquum* their axes are in a straight line, and the common vascular bundle, or stele, closely resembles that of *Ophioglossum Moluccanum*. The stele of the primary root, however, is diarch as it is in *B. Virginianum* and in most of the Marattiales.

The development of the cylindrical stele in the axis of the young sporophyte is essentially the same as in *B. Virginianum*, *i.e.*, it is formed by the union of the broad leaf traces of the early leaves.

The writer was not able to obtain the youngest stages of the sporophyte in Helminthostachys, but from a study of somewhat older specimens the conclusion was reached that the stele is formed in much the same way as in Botrychium.[16]

The Marattiales

Brebner[17] first called attention to the absence of a cauline stele in the young sporophyte of *Danaea simplicifolia*, although the writer[18] had shown in an earlier study on *Marattia* that there was at first a continuous procambium strand traversing the young cotyledon and primary root. Farmer's figures of the young sporophyte of Angiopteris[19] show the same condition. The most recent contribution to the subject is a paper by West[20] who finds that there is no cauline stele in the young sporophyte of the Marattiaceae.

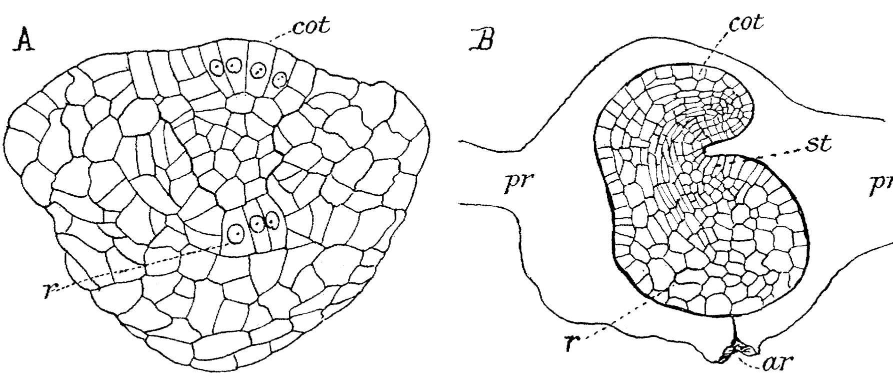

FIG. 5. *A*. Vertical section of an embryo of *Danaea elliptica*, passing through the cotyledon, and showing the endogenous origin of the root, *r*. *B*. A nearly median section of a very young sporophyte of *Marattia Douglasii*, showing the young stele extending from the cotyledon into the root. The root apex does not show in this section.

[16] Campbell. The Eusporangiatae.

[17] Brebner, *loc. cit.*

[18] Campbell, D. H. Observations on the development of *Marattia Douglasii*, Baker. Annals of Bot. **8**: 1–20. 1894.

[19] Farmer, J. B. The embryogeny of *Angiopteris evecta*, Hoffm. Annals of Bot. **6**: 265–270. 1892.

[20] West, *loc. cit.*

The writer[21] examined with great care the development of the fibro-vascular system in the young sporophytes of *Danaea Jamaicensis* Underw. and *D. elliptica* Smith, and also the younger stages of the sporophytes of species of Angiopteris, Kaulfussia, and Marattia. In all of these (fig. 5, *A*) it was found that the primary root is deep-seated, growing through the foot precisely as it does in *Ophioglossum Moluccanum* and *Botrychium obliquum*, and there is a single primary stele traversing the axis of the cotyledon and root (fig. 5, *B*). The young plant is thus bipolar, so far as the cotyledon and root are concerned, and the insignificant stem apex appears as a small lateral appendage near the junction of the two primary organs. No procambium can be made out in the very small mass of tissue which can be assigned to the stem.

This is particularly well shown in Danaea (fig. 6), where the stem apex is seen in the angle formed by the junction of the bundle from the second leaf with the primary bundle, but no sign of procambial tissue can be seen in the region above this junction.

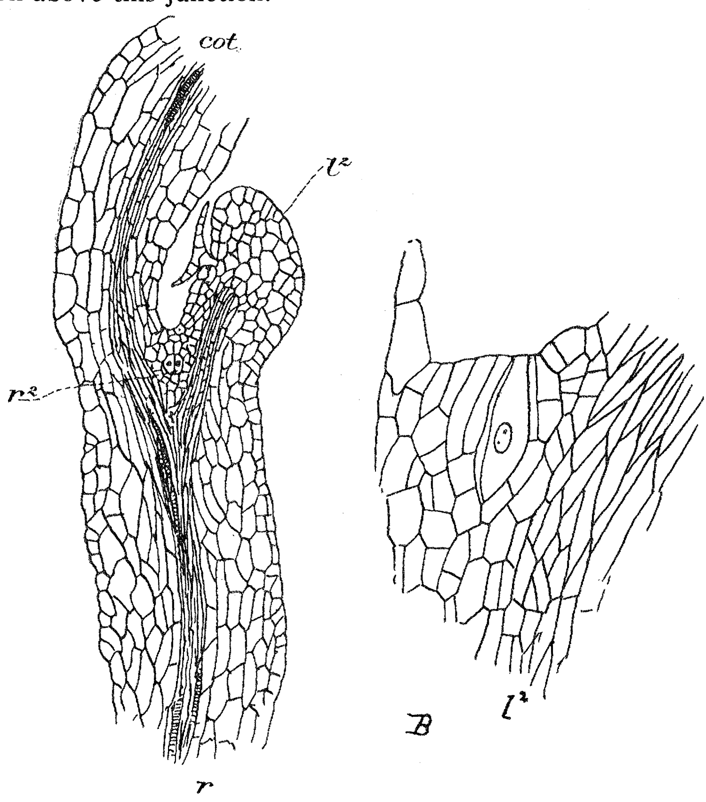

FIG. 6. *A*. Longitudinal section of young sporophyte of *Danaea elliptica*, showing the junction of the two leaf-traces. *B*. The stem apex of the same sporophyte with the trace of the second leaf, l^2, passing to one side of it.

[21] Campbell. The Eusporangiatae.

The vascular strands of the first two leaves are collateral in structure, and after their fusion near the junction of the cotyledon and primary root, the xylems of the two bundles are easily recognizable and are continuous with the two xylems of the diarch root (fig. 7).

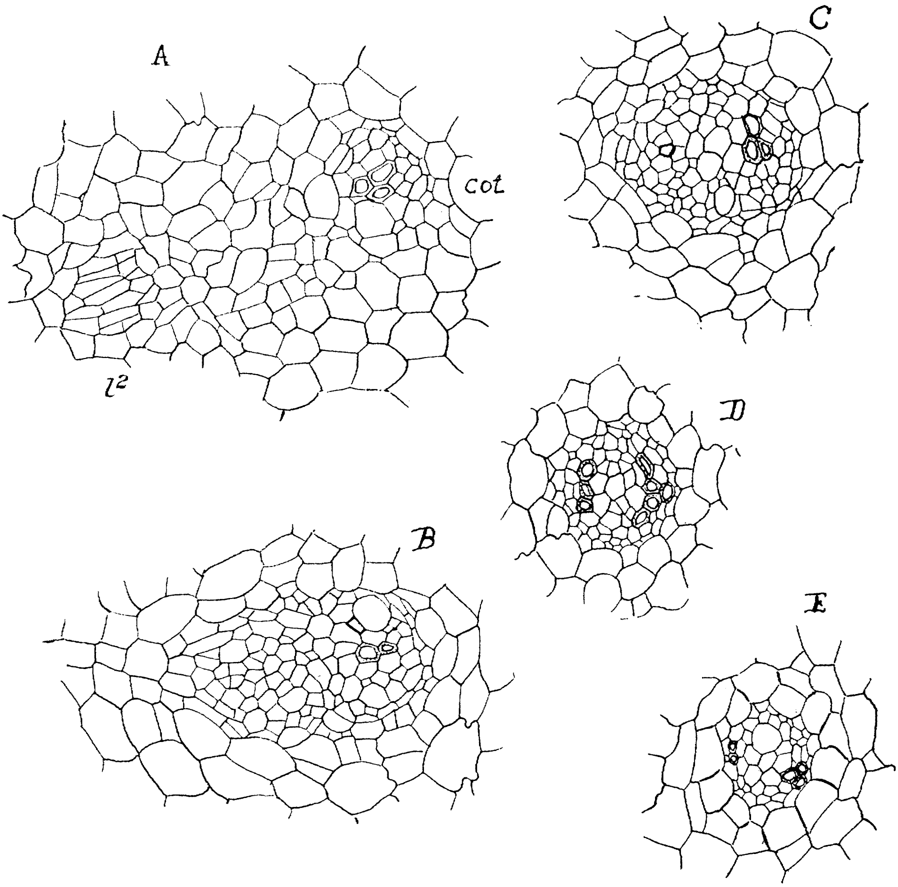

FIG. 7. Five cross sections of a series from a young sporophyte of *Danaea Jamaicensis*. *A* shows the two primary leaf-traces; *B* and *C*, the fusion of these to form the solid stele of the young plant; *D*, the transition region of the sporophyte; *E*, the stele of the root.

It is clear that the central region of the young sporophyte is not strictly a cauline structure, since the cotyledon and primary root are in no sense appendages of the stem, which at this stage consists only of the very small area in the immediate vicinity of the apical meristem. Moreover, the foot contributes a considerable amount of the outer tissue in the central region of the young sporophyte.

As the new leaves are formed, close to the stem apex, their steles unite with those of the older ones, and there is thus built up a "dictyostele," much like that in Ophioglossum. After about seven leaves have been

formed, this structure is complicated by the development of vascular strands inside the dictyostele, and these "commissural" strands can be traced up to the apical meristem of the stem, and are therefore true cauline strucures. As the sporophyte increases in size, the number of leaf-traces increases and further commissural strands are also formed, but the greater part of the elaborate skeleton of the adult sporophyte is undoubtedly of foliar origin, only the relatively unimportant commissural strands being cauline.

The history of the development of the fibro-vascular skeleton of the Eusporangiatae leads inevitably to the conclusion that in the Ophioglossales the whole stelar system is derived from the leaves and roots, and this is true to a great extent for the Marattiales, although in the latter the commissural strands are really cauline in origin.

It may be said also that the cortical tissue of the caudex is to a considerable extent of foliar origin, being made up of the coalescent leaf bases. This is, to some extent, a confirmation of Delpino's theory that the leaves, instead of being appendages of the stem, are the primary organs, and that the so-called stem is formed by the coalescence of leaf bases.[22]

It is also clear that the medullary tissue is in no case of stelar origin, but is always a portion of the ground tissue (to use the older term) which is more or less completely enclosed by the coalescent foliar steles.

The great preponderance of the foliar structures over the stem in most Filicineae has not received the attention that might be expected, in the many discussions on the nature of the stelar tissues that have appeared. Few of the higher plants show this to the same extent, and it may be questioned whether any Angiosperm can show leaves equal in complexity to such ferns as Angiopteris and some of the tree ferns. It is true that the leaves of some palms are bulkier, but structurally they are decidedly simpler. So far as mere length is concerned, probably some species of Gleichenia and Lygodium surpass even the longest palm leaf. Hooker[23] states that *Lygodium articulatum* A. Rich has stipes 50 to 100 feet in length arising from a slender prostrate rhizome.

The very young sporophyte of Ophioglossum, which the writer believes to be the most primitive of existing ferns, has no stem at all, but consists simply of a single leaf and root, the stem arising secondarily as an adventitious bud. This is entirely in harmony with the theory of the derivation of the Filicineae from Anthoceros-like ancestors; and the predominance of the leaf, shown in the young sporophyte, is maintained throughout the whole history of the Filicineae.

The assumption, therefore, that the stem is the predominant or primary organ of the sporophyte, and that the leaves are mere appendages of this, is hardly borne out by a study of the ontogeny, at least of the Eusporangiatae; and this probably will be shown also to be the case in many, at least, of the Leptosporangiatae.

[22] See Schoute, *loc. cit.*, p. 97.

[23] Hooker, J. D. Handbook of the New Zealand flora, p. 385. London, 1867.

When one compares the slender rhizome of such ferns as Lygodium, Gleichenia, and many Hymenophyllaceae with the large and highly developed leaves, it may well be questioned whether the leaves should be regarded as mere appendages of the relatively insignificant axis. This is particularly the case with such forms as Gleichenia and Lygodium whose leaves show almost unlimited power of continuous growth in length.

It is very important that further studies upon the origin of the stelar tissues of the Leptosporangiatae should be undertaken. Most of the studies already made upon the ontogeny of these ferns have not dealt with the earliest stages of the stelar tissues, but have started with the fully developed stele of the young sporophyte, assuming that this axial stele is really of cauline origin and not a composite structure derived from a fusion of leaf-traces. In order to solve this question it is necessary to examine series of sections, both transverse and longitudinal, including the growing point of the stem and the adjacent regions. In longitudinal sections alone there is danger of misinterpretation, as the traces of the youngest leaves may be easily mistaken for a true cauline stele; but if corresponding transverse sections are examined, it is then possible to determine whether or not there is a stele of strictly cauline origin.

It will not be surprising if such a test applied to the Gleicheniaceae and Hymenophyllaceae will show that the solid or tubular axial steles are in reality composed of coalescent leaf-traces as they are in Botrychium and in the young sporophytes of some of the Marattiales.

It is very desirable that the many careful studies of the stelar tissues of the ferns be reviewed to determine whether the usual interpretations of the relation of the tissues of the leaves and axis are tenable. A satisfactory solution of the problem necessitates an examination of the origin of the tissues in the young sporophyte as soon as it emerges from the gametophyte, and a further study of the building up of the stelar structures as new leaves are developed, tracing the origin of the individual vascular strands to their beginning. Reconstructions from series of cross sections of the completed bundles of older stages will not suffice.

Conclusion

The presence of a single cauline stele—"protostele," "siphonostele," "dictyostele"—is not borne out by the history of the stelar tissues in the Ophioglossales and Marattiales. In all of these the stelar system begins as a single strand common to the first leaf and root; the stem apex arises adventitiously in *Ophioglossum Moluccanum* and *O. pendulum*, and is very insignificant in Botrychium and the Marattiales. No procambium is developed in the stem region in the young sporophyte.

In the Ophioglossales, the stelar structures of the axis are built up exclusively of leaf-traces to which the bundles of the roots are joined. This condition obtains also for the earlier stages of the Marattiales, but is com-

plicated later by the formation of "commissural" strands, which are of cauline origin.

The "dictyostele" of Ophioglossum and most Marattiales is in no sense a monostele. The "foliar gaps" are not breaks in a single tubular stele, but are merely spaces between the coalescent leaf-traces, and the pith is part of the ground tissue included within the cylindrical network formed by the united bundles derived from the leaves.

In short, the condition found in the axis of the eusporangiate ferns is more in accord with the older theory of "common" bundles traversing a ground tissue, and united to form the woody cylinder of the axis, than with the assumption o a true cauline stele.

The condition existing in the eusporangiate ferns by no means implies that the stelar hypothesis must be completely discarded. There seems to be no question of its application to the Lycopods, Conifers, and many Angiosperms; but in all of these, the relative importance of stem and leaf is very different from the condition in the ferns; and it will not be surprising if, when the different types of the Leptosporangiatae are subjected to a thorough examination of the origin of the stelar tissues in the young sporophyte, it will be found that in these, as well as in the Eusporangiatae, the axial stelar tissues are largely, at least, of foliar origin.

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